ISSN 0753-4973

ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY



March 1995

Volume 13, N° 1

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ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY

March 1995 **Volume 13, N° 1**

Alytes, 1995, **13** (1): 1-13.

Description of a central Amazonian and Guianan tree frog, genus *Osteocephalus* (Anura, Hylidae), with oophagous tadpoles

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A new species of the hylid frog genus *Osteocephalus* is described from Manaus, Amazonas, Brazil. It is a medium-sized species that resembles *O. taurinus*, but is smaller and has shorter hind legs. In contrast to other species of *Osteocephalus*, the dorsal skin is barely sexually dimorphic and the male's vocal sac is single, median and subgular. The tadpole is peculiar for living in phytotelmes, feeding on conspecific eggs and having a labial tooth row formula of 2(2)/3.

Most species of the neotropical hylid frog genus *Osteocephalus* Steindachner, 1862 are identifiable by the presence of well-ossified skulls, the presence of paired lateral vocal sacs, and rugose or warty dorsal skin in males and relatively smooth skin in females. TRUEB & DUELLMAN (1971) reviewed and defined the genus and recognized five species: *O. buckleyi* (Boulenger, 1882), *O. leprieurii* (Duméril & Bibron, 1841), *O. pearsoni* (Gaige, 1929), *O. taurinus* Steindachner, 1862 and *O. verruciger* (Werner, 1901) (*verrucigerus* auct.). DUELLMAN (1974) followed COPE (1867) in placing *Hyla langsdorffii* Duméril & Bibron, 1841 in the genus. Topotypes of *Hyla elkejungingerae* Henle, 1981 were identified as *O. verruciger* by DUELLMAN (in litt. to W. BÖHME, pers. comm.) but placed into the synonymy of *O. taurinus* by HOOGMOED (in FROST 1985) and regarded as a distinct species, *O. elkejungingerae*, by HENLE (1992). MARTINS & CARDOSO (1987) described *O. subtilis* from Acre, Brazil, and DUELLMAN & HOOGMOED (1992) placed *Hyla rodriguezi* Rivero, 1968 in *Osteocephalus*. AYARZAGÜENA et al. (1992a) described five species, *O. aecii*, *O. edelcae*, *O. galani*, *O. luteolabris* and *O. rimarum* from Venezuelan table mountains and placed them in the *O. rodriguezi* group. AYARZAGÜENA et al. (1992b) transferred this group to a

new genus, *Tepuihyla*. Thus, between 7 and 14 described species are currently comprised in the genus.

An additional species from midwestern Amazonia is in the process of being described by M. MARTINS and M. GORDO (pers. comm.). One more species from central Amazonia and two Guyanese states has been known for much more than a decade and has appeared in the literature many times as *Osteocephalus* sp. (HOOGMOED, 1979; ZIMMERMAN, 1983; ZIMMERMAN & BOGART, 1984; MARTINS & CARDOSO, 1987; HERO, 1990; HÖDL, 1990, 1993; ZIMMERMAN & RODRIGUES, 1990; HOOGMOED & AVILA-PIRES, 1991; DUELLMAN & HOOGMOED, 1992; WEYGOLDT & JUNGFER, 1993) or erroneously as *Osteocephalus buckleyi* (ZIMMERMAN & BOGART, 1988). In the course of our independent work on the reproductive biology and tadpole morphology of this species, we felt that the taxonomic status of the frog needed to be resolved. Therefore we describe it here as

Osteocephalus oophagus sp. nov.

Holotype. — MZUSP 69852, an adult male, collected by K.-H. JUNGFER on 9 April 1993 at Reserva Florestal Adolfo Ducke (2°55'S, 59°59'W), situated at km 26 of the Rodovia AM-010 (Manaus-Itacoatiara), Estado do Amazonas, Brazil.

Paratypes. — NMW 32925.1-2, collected by W. HÖDL on 28 February 1978; MPEG 4845-4846, collected by M. J. HENZL, L. S. FORD and A. LIMA on 9 February 1992; AMNH A.136183-136184, collected by M. J. HENZL and L. S. FORD on 3 March 1992; MZUSP 69853, INPA 01446 and 01448, SMNS 10801-10802, ZFMK 57137-57138, all collected by K.-H. JUNGFER between January and April 1993; all from Reserva Florestal Adolfo Ducke. For sexes and Museum abbreviations see Table I.

Definition. — For purposes of comparisons, we follow TRUEB & DUELLMAN's (1971) standards. A medium sized species of *Osteocephalus* (maximum known snout-vent length (SVL) 47.2 mm in males, 62.7 mm in females). Dorsal skin in males with a few non-spinous tubercles or smooth, in females smooth. Skin on flanks smooth, slightly shagreened posterior to the insertion of the arm in some specimens. Webbing on hand moderate, up to first third of antepenultimate phalanx on inner edge of third finger. Dorsum brown to grey with or without irregular tan flecks, spots, mottling or reticulation, with white spots in some specimens. Venter white; in some specimens very light brown reticulation present on the chest. Lips brown or grey, with or without a cream subocular spot extending to the edge of the tympanum. Flanks brown or grey. White mottling or reticulation on posterior half of the flanks; many white spots on dark ground present in some specimens.

Diagnosis. — *Osteocephalus oophagus* is distinguished from the frogs of the *O. rodriguezi* group by substantial webbing on the hand (absent or rudimentary in the *O. rodriguezi* group), and from *O. buckleyi* by the lack of a conspicuous row of tubercles on the tarsus and prominent supraorbital tubercles. *O. verruciger* and *O. elkejungingerae* are larger and the dorsum of males is covered by many spinous tubercles. *O. leprieurii* has less webbing on the hands (web reaching base of antepenultimate phalanx on inner side of third finger) and in some cases transverse lines or bars on the dorsum that are absent in *O. oophagus*. *O. langsdorffii* is larger and has scalloped dermal folds on the outer edges of hands and

feet that are lacking in *O. oophagus*. The new species is distinguished from *O. pearsoni* by the lack of brown reticulation on the venter (present only in chest area, if at all, in *O. oophagus*) and more webbing on the hands (to base of antepenultimate phalanx on inner side of third finger in *O. pearsoni*). *O. subtilis* has a black iris (golden with black rays in *O. oophagus*) and a glandular line above the vent (absent in *O. oophagus*). An additional undescribed species from midwestern Amazonia bears a conspicuous, complete white line running around the whole of the upper lip (faint and interrupted in *O. oophagus*), and its supratympanic fold is smooth (tubercular in *O. oophagus*) (M. MARTINS, pers. comm.). *O. oophagus* is most easily confused with *O. taurinus*, with which it shares the golden iris with radiating black lines. *O. taurinus* is a larger frog that reaches 104 mm. The dorsum in males is covered by many spinous tubercles with keratinized tips. The webbing on the hands is slightly more extensive than in *O. oophagus*, reaching the middle of the antepenultimate phalanx on the inner side of the third finger. The legs are longer than in *O. oophagus*. When stretched forward and angled at 90° at the tibiotarsal articulation, the tarsus reaches the tip of the snout in *O. oophagus* and extends beyond that point in *O. taurinus*. Furthermore, adults of *O. taurinus* possess two elevated longitudinal bony ridges (frontoparietal flanges) in the interorbital area, that are not visible in *O. oophagus*, but may be felt in large specimens when rubbing with the fingertips.

Description of holotype. – Measurements and proportions (following DUELLMAN, 1970) are given in Tables I and II. A male of 43.8 mm SVL (fig. 1a). Body wider than the head. Diameter of the tympanum slightly wider than half the eye diameter. Head flat between orbits, slightly concave in the intercanthal region and truncate in lateral and dorsal aspect. Nostrils elevated, internarial region slightly depressed. Canthus rostralis slightly rounded, loreal region concave, bearing a few rounded warts below the canthus. An elevated dermal fold ascending posterior to the mid level of the eye to the area above the tympanum and sloping to the insertion of the arm. Tympanum distinct and rounded. A weak axillary membrane extending to less than one fifth the length of the humerus. A row of flat, barely raised warts visible on the ventrolateral edge of the forearm, extending onto the proximal half of the fourth finger. Fingers with moderately large discs, that of the third finger about four fifths the diameter of the tympanum. Enlarged prepollex bearing an elliptical tubercle. Nuptial pads absent (dark brown before), as the frog was no more in breeding condition when preserved on 28 July 1993. Distal subpalmar tubercle bifid on finger IV. Webbing basal between finger I and II and with a webbing formula (SAVAGE & HEYER, 1967; MYERS & DUELLMAN, 1982) of II1,5-3^{-}III2,5-2^{+}IV in the others. Relative finger lengths of adpressed fingers 3>4>2>1 (fig. 2a). Legs relatively short. Tarsus reaching the tip of the snout when stretched forward parallel to the body axis and bent at 90° at the tibiotarsal articulation. Inner metatarsal tubercle large, flat and elliptical. No outer metatarsal tubercle. Toe webbing formula I1^{+}-2^{-}II1^{+}-2III1^{+}-2IV2-1^{+}V. Relative toe lengths 4>5>3>2>1 (fig. 2b). Vent opening positioned posteriorly at the upper level of the thighs.

Dorsally, skin weakly granular with low tubercles in the inter- and postorbital region and few on the anterior part of the dorsum. Dorsal aspects of the arms weakly granular and those of the legs smooth. Laterally, skin tubercular posteroventral to the tympanum, shagreened on the anterior half of the flanks and smooth on the posterior half, tubercular

Table I. - Measurements of type specimens of *Osteocephalus oophagus*. Measurements in mm: ED, eye diameter; FL, foot length; HL, head length; HW, head width; SVL, snout-vent length; TL, tibia length; TD, tympanum diameter. Museum abbreviations: AMNH, American Museum of Natural History, New York; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MPEG, Museu Paraense Emilio Goeldi, Belém; MZUSP, Museu de Zoologia, Universidade de São Paulo; NMW, Naturhistorisches Museum Wien; SMNS, Staatliches Museum für Naturkunde, Stuttgart; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

	SVL	HL	HW	ED	TD	TL	FL
Males							
SMNS 10802	35.7	12.2	10.7	3.90	2.16	19.5	13.8
MPEG 4846	41.6	14.5	13.7	4.80	3.12	23.5	17.5
INPA 1448	42.3	14.2	13.1	5.10	2.82	22.8	15.8
AMNH 136184	42.5	15.2	13.8	5.10	2.86	24.2	17.8
NMW 32925.2	43.2	14.6	13.9	4.86	2.82	22.7	17.0
ZFMK 57138	43.3	15.5	14.5	5.22	3.24	24.3	17.9
MZUSP 69852	43.8	14.7	13.0	4.56	2.52	23.3	17.2
SMNS 10801	47.2	16.6	14.6	6.00	3.66	23.5	18.3
Females							
AMNH 136183	46.2	16.0	13.7	5.34	3.20	23.8	18.1
ZFMK 57137	49.8	17.2	16.9	5.34	3.48	27.7	20.3
MPEG 4845	53.2	18.2	16.9	5.52	3.96	29.5	22.5
MZUSP 69853	53.6	17.9	16.7	5.82	3.90	30.8	21.2
NMW 32925.1	54.6	18.9	16.5	5.46	4.32	31.2	22.0
INPA 1446	55.6	17.7	16.8	5.10	3.72	29.5	21.6

Table II. - Proportions of male and female *Osteocephalus oophagus*. Abbreviations: see Table I.

Locality, sex	*n*		HL / SVL	HW / SVL	TD / ED	TL / SVL	FL / SVL
Reserva Ducke, males	8						
		min.	0.336	0.297	0.553	0.498	0.374
		max.	0.358	0.335	0.650	0.569	0.421
		mean	0.346	0.316	0.585	0.542	0.399
Reserva Ducke, females	6						
		min.	0.318	0.297	0.599	0.515	0.388
		max.	0.346	0.339	0.791	0.575	0.423
		mean	0.339	0.312	0.693	0.551	0.402
Rio Urucu, females	2						
		min.	0.348	0.297	0.735	0.557	0.403
		max.	0.357	0.301	0.835	0.574	0.418
		mean	0.353	0.299	0.785	0.566	0.411

below the vent. Skin on the belly and the posteroventral thigh surfaces granular, the other ventral surfaces smooth. Tongue round. Prevomers angular, with 8 and 10 prevomerine teeth. Vocal slits extending postero-laterally from the middle of the tongue. Vocal sac subgular, median and weakly distensible during call.

Colour in alcohol. — Dorsal surfaces brown with tan flecks and blotches. Flanks light brown with brown mottling on the posterior half. Upper and lower lips bordered by faint creamy stripes often interrupted by tan spots. Venter creamy with some faint light brown mottling on the chest. Throat creamy white with light brown mottling. Ventral surfaces of the arms creamy with a brown hue, those of the legs pale light brown. Posterior thigh surfaces brown. Bones green and visible through the skin. Iris yellowish white with many radiant black stripes and a horizontal black bar on each side of the pupil.

Colour in life. — Depending on illumination and colour of the substrate the frog was sitting on, the dorsal colour varied from light brown with indistinct darker flecks and blotches to dark brown with almost black flecks and blotches. Flanks were brown to creamy brown with darker brown mottling on the posterior half. Ventral surfaces were white. Bones were green and the iris golden yellow with radiant black stripes and horizontal black bars.

Variation. — The largest male of the type series has an SVL of 47.2 mm, the largest female of 55.6 mm. Thirty marked and released males from the type locality bearing nuptial pads ranged from 35.9 to 45.5 mm, and seventeen ovigerous females from 49.8 to 60.6 mm. One female (INPA 01442) from the Rio Urucu is 62.7 mm. There is little variation in proportions between the sexes, except that the tympana of females are slightly larger than those of males (Table II). The dorsal skin varies from smooth to weakly granular, bearing none or a few raised tubercles. There is a tendency of males to bear a few more tubercles on head and dorsum than females, but some males have both surfaces smooth, while some females have a few tubercles on the head and sometimes on the dorsum. This variation is found in the preserved material at hand, and was also obvious in the many live frogs we saw. Dorsal tuberculation is not a reliable sexual dimorphic character. Breeding males bear horny dark brown nuptial pads on the prepollices.

A lot of variation was observed in coloration. In preservative, the dorsal colour ranges from grey to dark brown with or without darker blotches or flecks (figs. 1a-b). Also, the amount of cream spots or mottling dorsally, laterally and around the vent is variable (figs. 1c-d). The ventral brown mottling on chest and throat may be lacking or reduced to the area under the lower jaw.

Habitat. — Reserva Florestal Adolfo Ducke, a reserve managed by the Instituto Nacional de Pesquisas da Amazônia (INPA), consists of hilly terra firme lowland forest at an altitude of about 50 m. Frogs usually migrate at night on vertical stems of young trees and bushes normally less than 2 cm in diameter at heights of 0.5 to 2 m. Males call from near or inside phytotelmes.

Reproductive biology. — Pairs of *O. oophagus* deposit their eggs in phytotelmes, such as epiphytic or ground bromeliads, Buriti Palm (*Mauritia flexuosa*) leaf axils, water-filled palm bracts lying on the ground or tree holes up to heights of about 35 m. Females return to the deposition sites regularly in intervals of about five days, usually clasped by the same

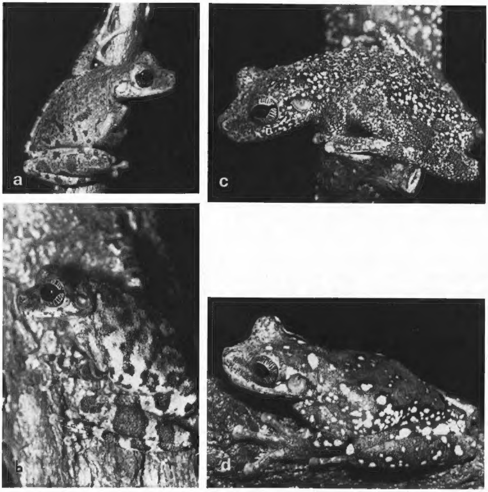


Fig. 1. — *Osteocephalus oophagus* sp. nov. Specimens from the type locality. (a) Holotype MZUSP 69852, adult male. (b) Male showing numerous tan dorsal blotches. (c) Subadult female with numerous small white spots. (d) Adult female showing extreme extent of lateral and dorsal white spots.

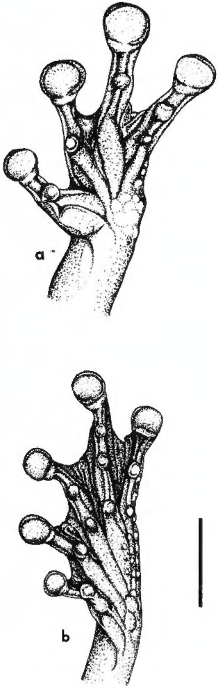


Fig. 2. — Hand (a) and foot (b) of a male *Osteocephalus oophagus* (paratype INPA 01448). Line equals 5 mm.

males. If there are larvae already present, they consume the newly laid eggs. The eggs not eaten hatch. The larvae starve if the mother fails to return and if they are not provided with trophic eggs (WEYGOLDT & JUNGFER, 1993). A detailed study on the reproductive biology is in progress.

Calls. — The advertisement call usually consists of one to six croaking notes emitted at night and occasionally during the day (type A). At night it is very often followed by one to four (usually two) distinctly different notes that sound like "ka ká" (type B).

Type A of frogs from the INPA-WWF MCSEP reserves and from Parque Nacional Tapajós were described in detail by ZIMMERMAN & BOGART (1984), who recorded an emphasized frequency of 1.62 ± 0.65 kHz, low frequency range of 0.89 ± 0.33 kHz, high frequency range of 2.84 ± 0.42 kHz, and call duration per note of 0.24 ± 0.07 s. ZIMMERMAN & BOGART (1988) again described calls and calling of this frog, under the name of *Osteocephalus buckleyi*. They noted the high intraspecific variability and other characteristics of the call.

Description of the tadpole. — Tadpoles were collected by L. C. SCHIESARI on 5 March 1993 in water-filled plastic basins used as egg-laying sites by *O. oophagus* near the Igarapé Acará, Reserva Florestal Adolfo Ducke, and preserved in 10 % formalin. Two tadpoles were raised until metamorphosis. Measurements were taken with the optical measuring unit Wild MMS 235. Drawings (figs. 3-4) were made with a camera lucida attached to a stereomicroscope. Measurements were made according to GRILLITSCH et al. (1993). Developmental stages were determined following GOSNER (1960). Labial tooth row formula (LTRF) is after ALTIG (1970). The following description is based on 10 tadpoles ranging from stage 35 to stage 38. Measurements of larvae are given in Table III.

Tadpole of ORTON's (1953) type IV. Body slightly depressed, ovoid in dorsal view. Snout nearly truncate from above and, in profile, acutely rounded. Eyes positioned dorsolaterally; interorbital distance 1.5-1.7 times the internarial distance, which in turn equals width of oral disc. Nares rimmed, rounded, and directed anterolaterally. Their distance to the eyes about half of their distance to tip of the snout. Spiracular tube sinistral, ventrolateral, and directed posterodorsally. Spiracular opening slightly posterior to mid length of body, to which it is tightly attached. Dorsal and ventral margin of caudal musculature parallel in proximal third, then gradually narrowing and almost reaching tip of the tail. Ventral fin slightly lower than dorsal one, fairly paralleling ventral margin of caudal musculature. Dorsal fin extending a short distance onto body. Oral disc anteroventral and not emarginate. One row of moderately sized marginal papillae with a medial gap in upper labium which may be visible in dorsal view. Submarginal papillae in some specimens in one discontinuous row in lower labium as well as scattered in ventrolateral portion of oral disc. Two rows of denticles on the upper labium, the second one showing a distinct median gap, and three rows on the lower one (LTRF 2(2)/3). Upper jaw sheath arched, lower one V-shaped, both black and without serrations (magnification 50 ×). Colour of measured tadpoles chestnut brown dorsally; venter and caudal musculature lighter.

Ontogenetic change. — Newly metamorphosed frogs 12-13 mm in SVL and completely different in colour from the adults. Dorsal and lateral surfaces grey except for a black canthal stripe continuing as a supratympanic stripe posterior to eye to insertion of the arm. Dorsal surfaces of upper arm and proximal half of lower arm white. An orange spot on

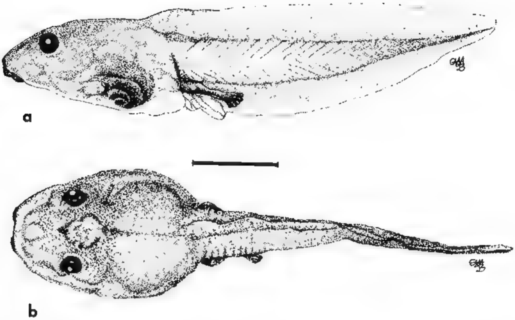


Fig 3 - Dorsal (a) and lateral (b) view of a tadpole of *Osteocephalus oophagus* in stage 36 (GOSNER, 1960) of typical proportions Line equals 5 mm.

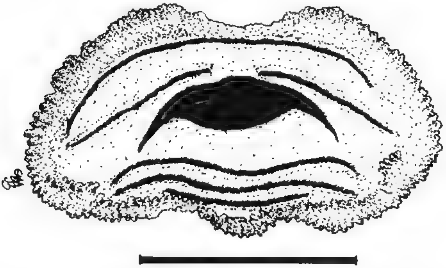


Fig 4. – Oral disc of a tadpole of *Osteocephalus oophagus* (same individual as in fig. 3). Line equals 1.4 mm.

Table III. - Measurements of larvae of *Osteocephalus oophagus* (mean values, ranges in parentheses). Measurements in mm: DT, maximum height of tail; LF, maximum height of lower (ventral) tail fin; SVL, snout-vent length; TL, total length; UF, maximum height of upper (dorsal) tail fin; VT, tail length.

Stage	*n*	TL	SVL	VT	DT	UF	LF
19	1	4.66					
20	4	4.73 (4.35-5.03)					
23	5	5.98 (5.70-6.48)					
27	1	16.7	7.2	9.5	3.71	1.20	1.19
28	1	19.5	8.6	10.9	4.68	1.61	1.50
30	1	21.3	9.1	12.2	4.97	1.60	1.62
31	1	24.2	10.2	14.0	5.21	1.61	1.58
33	2	26.2 (25.4-27.0)	11.7 (11.6-11.8)	14.5 (13.8-15.2)	6.02 (5.93-6.10)	1.98 (1.86-2.10)	1.76 (1.76-1.76)
34	2	23.7 (22.5-24.9)	10.8 (10.1-11.4)	12.9(12.4-13.5)	5.83 (5.31-6.34)	1.74(1.59-1.89)	1.81 (1.73-1.88)
35	5	27.0 (25.0-28.2)	12.5 (10.0-13.3)	14.5 (12.8-16.0)	6.14 (5.84-6.44)	1.99 (1.90-2.14)	1.84 (1.66-2.02)
36	1	28.9	14.2	14.7	6.49	2.08	1.75
37	1	27.8	12.9	14.9	6.55	2.08	1.98
38	3	29.5 (26.4-31.6)	13.9 (13.6-14.5)	15.5 (11.9-17.8)	6.44 (6.44-6.44)	2.06 (1.98-2.13)	1.94 (1.88-1.99)
39	3	30.0 (28.4-31.4)	13.8 (13.4-14.3)	16.2 (15.0-17.6)	6.96 (6.27-7.85)	2.07 (1.84-2.35)	1.91 (1.60-2.16)
40	2	34.6 (32.9-36.2)	15.1 (15.0-15.1)	19.5 (17.8-21.2)	6.78 (6.65-6.90)	1.96 (1.57-2.35)	1.99 (1.95-2.04)

elbow, distal dorsal surface of lower arm and proximal dorsal surface of fourth finger. A large white spot, capped by a smaller orange one, on heel. Another orange spot on knee and in some specimens on outer edge of the metatarsus. Finger- and toe-discs orange. Iris bright red without radiating black stripes. With this colour pattern, they are virtually indistinguishable from sympatric *O. taurinus* (juveniles described as *O. taurinus* by Duellman & Lescure, 1973, are most likely those of *Hyla geographica*).

A specimen of 21 mm SVL already had the typical adult pattern, except that the white spot on the upper arm and proximal lower arm was still present. The finger- and toe-discs, as well as the iris, already with black rays and horizontal bars, had an orange hue.

Distribution. — Apart from the Reserva Ducke, about 25 km north of Manaus, we have heard the distinctive call of this species in the forest of the Universidade do Amazonas campus within the city of Manaus and in Reserva Florestal Walter Egler, about 50 km north-northeast of Manaus. The frog is well known from the INPA-WWF Minimal Critical Size of Ecosystems Project (MCSEP) reserves, approximately 80 km northeast of Manaus (Zimmerman, 1983; Zimmerman & Bogart, 1984, 1988, Zimmerman & Rodrigues, 1990). Hoogmoed (1979) listed it from "eastern Guiana" and Hoogmoed & Avila-Pires (1991) recorded it from Petit Saut, French Guyana, and remarked that it was also known from Suriname and Brazil. Those records are all in the Guianan biogeographical region (see Hoogmoed, 1979 for a delimitation). We have not found or heard the species just south of the Amazon in the forests along the Manaus-Humaitá road, but M. Martins and M. Gordo (pers. comm.) found specimens at the Rio Urucu about 100 km

SSE of Coari. It has also been recorded from the Parque Nacional do Tapajós near Itaituba, southwest of Santarém, Pará (ZIMMERMAN & BOGART, 1984).

Discussion. — The new species possesses a number of characters new or unusual for the genus. In their definition, TRUEB & DUELLMAN (1971) (slightly altered by DUELLMAN & HOOGMOED, 1992) found *Osteocephalus* to have "vocal sacs paired, posterior, and when inflated protruding posteroventral or posterolateral to angles of jaws". *Osteocephalus oophagus* has a single median subgular vocal sac, a character shared with some frogs of the *O. rodriguezi* group (sensu AYARZAGÜENA et al., 1992a) (AYARZAGÜENA et al., 1992b). Also, it is similar to some frogs of that group in that the dorsal skin structure is not a reliable sexually dimorphic character (AYARZAGÜENA et al., 1992a). Although males tend to be slightly more granular, there are smooth skinned males both alive and especially in preservative.

Tadpoles have two upper and three lower tooth rows like most lentic hylid larvae. In other species of *Osteocephalus*, however, there are 2-3 upper and 5-8 lower tooth rows (HENLE, 1981; HERO, 1990). The reduction of denticle rows in *O. oophagus* may be an adaptation for oophagy as a special case of macrophagy. The tadpoles do not need to rasp their food as grazers. This might also be the reason for the absence of beak serrations. The reduction of denticle rows is known for many other arboreal tadpoles (LANNOO et al., 1987) and does not oppose its inclusion in the genus *Osteocephalus*.

Despite the differences mentioned above, *O. oophagus* shares important characters with *O. taurinus*: the juvenile colorations and the colour of the iris in adults are identical The frontoparietal flanges are present, though less conspicuous in *O oophagus*. For these reasons the new species may be most closely related to *O. taurinus*.

Derivatio nominis. The specific name *oophagus* is a compound of the Greek *oon* (egg) and *phagein* (to eat) and refers to the larval habit of eating conspecific eggs.

RESUMEN

Osteocephalus oophagus sp. nov. de Reserva Ducke, Manaus, Amazonas, Brasil, especie mediogrande del género, es semejante a *O. taurinus* pero más pequeña y con las piernas posteriores más cortas. En contraste a otros *Osteocephalus*, la piel dorsal no muestra dimorfismo sexual y el saco vocal del macho es impar, mediano y subgular. El renacuajo es atípico para este género, porque vive en fitotélmata, alimentándose de huevos coespecíficos y teniendo una fórmula de dentículos labiales de 2(2)/3. La especie es conocida de las bajas Guianas y de la baja Amazonía.

ACKNOWLEDGEMENTS

K.-H. JUNGFER's stay at the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, was supported by a grant of the Deutsche Forschungsgemeinschaft (Peter WEYGOLDT, principal investigator) L C SCHIESARI was partially granted by FAPESP (São Paulo Government Funding Agency), process 91/1131-0. We are grateful to Cornelia ADELMANN and Gustavo DE MATTOS

Accacio for executing the drawings, to Martin J. Henzl for the opportunity of searching with him south of the Amazon, to Wolfgang Böhme, Alain Dubois, Britta Grillitsch, Marcio Martins and Andreas Schlüter, who also translated the summary, and two anonymous reviewers, for critically reviewing the manuscript, to T. C. S. Avila Pires (MPEG), S. G. Egler (INPA), C. W. Myers (AMNH) and F. Tiedemann (NMW) for the loan of specimens in their care. Karin and Helmut Mägdefrau helped once again with unavailable literature. Logistical support was received through the INPA Department of Ecology. Our special thanks go to Walter Hödl, who is responsible for and initiated our interest in this frog.

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Reassessment of central Peruvian Telmatobiinae (genera *Batrachophrynus* and *Telmatobius*). I. Morphometry and classification

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The taxonomic status of the central Peruvian Telmatobiinae is reassessed by analyzing the intraspecific variation of 18 morphometric measures among the currently recognized taxa (3 genera, 6 species, 9 subspecies). Cluster analysis, principal component analysis and discriminant analysis lead to the recognition of two genera (*Batrachophrynus* and *Telmatobius*) including six species (*Batrachophrynus brachydactylus, B. macrostomus, Telmatobius brevirostris, T. carrillae, T. jelskii, T. rimac*) without segregation in subspecies. Two diagnostic external features distinguish *Batrachophrynus* from *Telmatobius* species, another two characters are convergent adaptations distinguishing the stream-inhabiting ecotype from the lake-inhabiting one.

INTRODUCTION

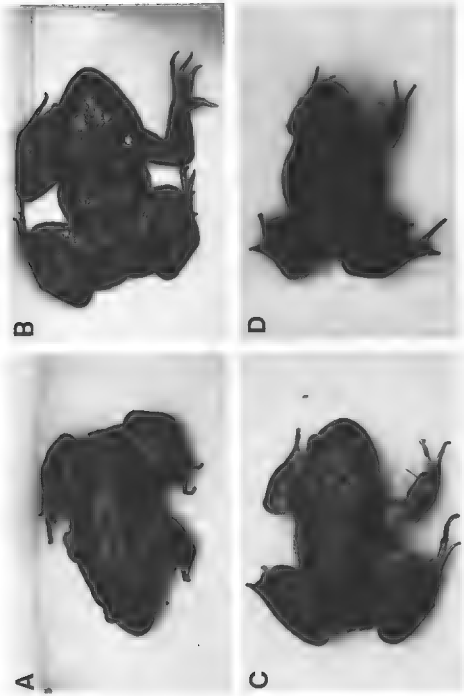
Leptodactylid frogs of the genus *Telmatobius* Wiegmann, 1835 inhabit the whole range of the Andes from Ecuador in the north to Chile/Argentina in the south (FROST, 1985; CEI, 1986). However, in the high-Andean regions of central Perú around Lake Junin (FJELDSA, 1983), two endemic *Telmatobius*-like species have been described as members of the genus *Batrachophrynus* Peters, 1873: the large lake-inhabiting Junin frog *B. macrostomus* and the stout stream-inhabiting *B. brachydactylus*. PETERS's (1873) distinction was based solely on the presence (*Telmatobius*) or absence (*Batrachophrynus*) of maxillary and prevomerine teeth. Yet, *T. brevipalmatus*, *T. edentatus* and *T. intermedius* lack maxillary teeth (LYNCH, 1971). Differences in several osteological characters other than teeth between *Batrachophrynus* and *Telmatobius* confirmed the generic distinction (LYNCH, 1978) and indicated an early separation of *Batrachophrynus* from the *Telmatobius* stock (CEI, 1986). LAURENT (1983) assigned *B brachydactylus* to a monotypic third genus *Lynchophrys* based on morphometric differences from *B. macrostomus*. At present, this view on taxonomy is maintained, though independent support is absent (DUELLMAN, 1993; FROST, 1985; LAVILLA, 1988a). According to LAURENT's opinion, *Lynchophrys* is more recently derived from the *Telmatobius* stock than is *Batrachophrynus*. Thus, the

phylogenetic relationship among the two species *B. brachydactylus* and *B. macrostomus* and of both with the genus *Telmatobius* are controversial.

The central Peruvian *Telmatobius* presently include four stream-inhabiting species, *T. brevirostris* Vellard, 1955, *T carrillae* Morales, 1988, *T. jelskii* (Peters, 1873) and *T. rimac* Schmidt, 1954, whereas *T. juninensis* (Shreve, 1938) was an incorrectly classified *Phrynopus* (DUELLMAN, 1993). VELLARD (1955) proposed three subspecies for *T. brevirostris*, four for *T. jelskii* and two for *T. rimac*, although the significance of the morphometric differences between the proposed subspecies was not tested for, and the existence of intermediate individuals was stated. Field studies in the Mantaro Valley (Department of Junín, Perú) on *T. jelskii* raised doubts on the subspecific classification because morphs pertaining to different "subspecies" were found within the same population (SINSCH, 1985, 1986, 1990).

Part of the taxonomic confusion in this group is probably due to morphological convergence among the species of each ecotype: the stream-inhabiting, semiaquatic frogs are stout and usually moderate-sized or small, whereas the lake-inhabiting, fully aquatic frogs are large (SINSCH, 1986, 1990). Therefore, phenotypic similarity between different species may reflect convergent adaptation to the same environmental factor rather than phylogenetic relationship. On the other hand, subtle differences among populations of the same species could result from direct responses to such factors as the amount of water flow in different streams. To test for environmental influences on morphological traits, we complemented our analysis of the two *Batrachophrynus* species and four stream-inhabiting *Telmatobius* species from central Perú with the lake-inhabiting Titicaca frog *Telmatobius culeus* (Garman, 1875) from southern Perú.

It is obvious that the validity of the central Peruvian taxa of Telmatobiinae needs to be confirmed by a thorough investigation. The definition of most taxa is exclusively based on morphological and morphometric characters (e.g. VELLARD, 1951, 1953, 1955) without an appropriate assessment of the intraspecific variation (TRUEB, 1979). Currently, the identification of most species is only possible by comparison with type specimens Consequently, our investigation evaluates VELLARD's type material in MHNSM (Museum of Natural History "Javier Prado", Lima, Perú) in comparison with the preserved specimens in URP (Museum of Natural History of the Ricardo Palma University, Lima, Perú) and with specimens collected in the field in 1992. We use cluster analyses to detect intraspecific morphological traits within the data sets of phenotypes described by morphometric characters. At the species level we widely follow the procedures used by WIENS (1993) in his recent taxonomic revision of the Telmatobiinae from northern Perú. Principal component and discriminant analyses are applied to quantify the differentiation among the seven nominal species. Finally, the differences among the genera and the ecotypes (stream- versus lake-inhabitants) are surveyed in discriminant analyses. The aims of our study are to provide an objective basis for the identification of central Peruvian Telmatobiinae and to distinguish convergent morphological traits from morphometric features which characterize species and/or genera.



A
B
C
D



Fig. 1 *Batrachophrynus brachydactylus* (A, dorsal view; E, ventral view); *B. macrostomus* (B, F); *Telmatobius jelskii* (C, G); *T. rimac* (D, H).

MATERIAL AND METHODS

The material examined included a total of 280 adult frogs pertaining to the seven nominal species *Batrachophrynus brachydactylus* (figs. 1A, 1E), *B. macrostomus* (figs. 1B, 1F), *Telmatobius brevirostris*, *T. carrillae*, *T. culeus*, *T jelskii* (figs. 1C, 1G) and *T. rimac* (figs. 1D, 1H). The frogs had been collected at 32 localities (fig. 2). The assignment of specimens to subspecies and to localities is listed in Appendix I, the number of individuals studied and the sex-specific size are given in Table I.

Standard morphometric measurements (nearest 0.1 mm) include: (1) snout-vent length (SVL); (2) height of body at the pectoral girdle (BH); (3) maximum width of head (HWID); (4) eye diameter (EYE); (5) interorbital distance (IOD); (6) eye-nostril distance, from anterior margin of eye to posterior edge of naris (ENOSE); (7) distance between the eye and the tip of the snout (ESNOUT); (8) humerus length (HUML); (9) radioulnar length (RADL); (10) hand length (HNDL); (11) length of the third finger (FG3L); (12) femur length (FEML); (13) tibia length (TIBL); (14) foot length, from union with tibia to the tip of fourth toe (FOOTL); (15) length of first toe (TOE1L); (16) length of fourth toe (TOE4L); (17) length of callus internus (CIL); (18) maximum length of toe web (WEBL).

Multivariate analyses were performed on $\log_{10}$-transformed data (BOOKSTEIN et al., 1985) and morphometric ratios The empiric measurements were transformed to ratios (range: 0-1) by calculating measures relative to SVL (SCHNEIDER et al., 1992, 1993). Moreover, two indices were used for further analysis: CIL/TOE1L and FEML/TIBL. Table II gives the means (and corresponding standard deviation) of these 19 relative measures for each species.

Due to the low number of individuals assigned to type material, we analysed the morphometric similarity between individuals in a cluster analysis using hierarchical grouping of the SVL-standardized phenotypes (WARD, 1963). This procedure subsequently reduces the number of groups by joining that specimen to another one or to a cluster which originates the lowest error sum of square. The result is a dendrogram based on phenetic similarity. As the proposals of subspecies by VELLARD were exclusively based on external morphology, valid subspecific taxa are expected to form homogeneous clusters.

At the species level, sets of the $\log_{10}$-transformed data were subjected to principal component analysis to explore the morphometric variability independent of taxonomic assignment. Principal components (PC) are linear combinations of the measured variables, uncorrelated with each other and explaining the maximum amount of variation. The first principal component (PC1) of morphometric data generally describes differences in size, but size effects may be present in subsequent principal components (HUMPHRIES et al, 1981). Techniques such as shearing have been developed to correct PC2 and PC3 for possible size effects (BOOKSTEIN et al., 1985), but they are controversial and size effects may still persist (ROHLF & BOOKSTEIN, 1987). Moreover, we applied canonical discriminant analysis to distinguish between the taxonomic groups delimited a priori. The resulting discriminant functions (CAN = canonical variables) are linear combinations of the measured variables that maximize the differences between the groups Discriminant

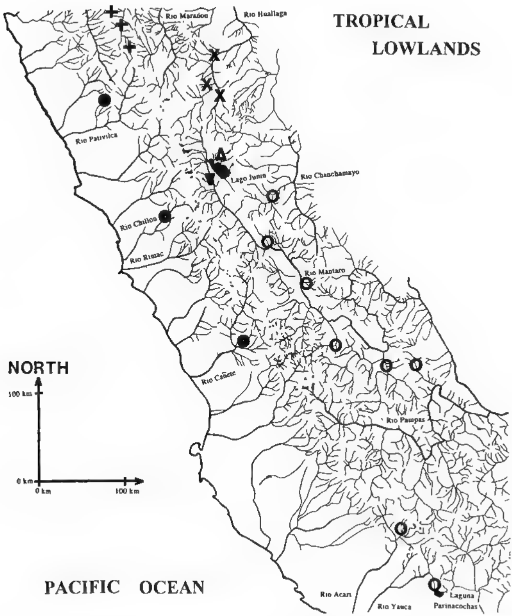


Fig. 2. — Distribution of the central Peruvian Telmatobiinae: *Batrachophrynus brachydactylus* (inverted triangle), *B. macrostomus* (open triangle), *Telmatobius brevirostris* (×), *T. carrillae* (+), *T. jelskii* (circles), *T. rimac* (dots). Localities are approximated from distances by roads, multiple localities in close proximity are represented by a single symbol. The main Andean river systems are indicated.

Table 1. Morphometric data for *Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris*, *T. carrillae*, *T. culeus*, *T. jelskii* and *T. rimac*. The first line is mean ± 1 SD; second line is range. All values are in millimeters; see text for abbreviations of variables.

Character	*B. brachydactylus*		*B. macrostomus*		*T. brevirostris*		*T. carrillae*		*T. culeus*		*T. jelskii*		*T. rimac*	
	Males N = 29	Females N = 24	Males N = 6	Females N = 7	Males N = 2	Females N = 3	Males N = 32	Females N = 21	Males N = 19	Females N = 23	Males N = 37	Females N = 35	Males N = 26	Females N = 16
SVL	56.5 ± 6.3	57.3 ± 5.6	130.0 ± 8.9	133.0 ± 17.2	57.7	59.4	43.3 ± 4.7	47.9 ± 3.7	93.4 ± 15.6	90.5 ± 23.5	54.4 ± 4.1	54.8 ± 5.4	49.8 ± 4.3	58.2 ± 10.9
	47.7 - 71.9	44.9 - 69.4	117.5 - 141	117.7 - 170.3	57.0 - 58.3	50.4 - 76.3	35.3 - 52.4	41.2 - 55.9	57.0 - 116.4	50.7 - 119.0	46.7 - 61.9	43.9 - 71.2	42.0 - 57.2	47.0 - 86.9
BH	11.1 ± 2.2	10.6 ± 2.9	23.0 ± 4.6	23.4 ± 4.8	16.4	17.1	10.2 ± 1.5	10.9 ± 1.2	26.2 ± 4.7	27.9 ± 9.2	13.6 ± 1.4	13.9 ± 1.6	11.8 ± 1.6	14.3 ± 3.4
	7.1 - 15.0	7.4 - 17.9	18.2 - 29.9	18.3 - 33.0	15.2 - 17.5	13.0 - 23.2	6.0 - 14.0	8.3 - 12.7	16.3 - 35.0	13.0 - 41.2	10.2 - 15.9	11.2 - 16.4	8.6 - 14.7	10.8 - 23.5
HWID	12.1 ± 1.9	17.4 ± 1.6	50.8 ± 4.7	55.4 ± 9.3	18.7	21.8	13.3 ± 1.5	14.1 ± 1.2	36.9 ± 7.7	36.6 ± 11.4	19.6 ± 1.8	20.2 ± 2.3	16.6 ± 1.4	20.0 ± 5.0
	15.0 - 24.3	15.2 - 20.5	46.1 - 57.4	46.4 - 75.3	17.4 - 20.0	17.0 - 30.1	10.4 - 16.2	11.5 - 17.0	21.3 - 51.9	16.8 - 51.7	15.7 - 23.3	15.1 - 25.7	13.8 - 18.3	14.4 - 31.6
EYE	4.9 ± 0.7	4.7 ± 0.6	8.2 ± 1.4	7.6 ± 0.7	5.8	6.2	3.8 ± 0.7	3.9 ± 0.5	7.0 ± 1.0	6.8 ± 1.2	5.3 ± 0.8	5.5 ± 0.8	5.4 ± 0.6	5.7 ± 0.9
	3.2 - 6.8	3.7 - 6.2	6.0 - 10.0	6.6 - 8.8	5.8 - 5.8	5.1 - 8.3	2.7 - 6.1	3.0 - 5.6	4.3 - 8.9	4.5 - 8.3	4.2 - 7.0	3.5 - 7.0	4.6 - 6.9	4.8 - 8.1
IOD	13.7 ± 1.0	13.3 ± 0.9	30.8 ± 2.4	32.0 ± 4.8	16.4	16.4	10.8 ± 1.1	11.0 ± 0.8	22.4 ± 3.4	21.6 ± 5.4	14.5 ± 1.6	14.8 ± 1.4	14.2 ± 1.[illegible]	15.9 ± 2.8
	11.7 - 15.6	11.7 - 15.2	27.7 - 33.9	28.4 - 42.5	15.9 - 16.9	14.4 - 20.4	7.4 - 13.4	9.1 - 12.6	14.2 - 27.1	12.0 - 28.7	11.4 - 20.2	11.0 - 17.7	12.6 - 16.1	13.1 - 23.8
ENOSE	8.7 ± 1.3	8.3 ± 0.6	18.4 ± 1.4	19.2 ± 2.6	9.5	10.0	6.9 ± 1.3	6.8 ± 0.5	12.4 ± 1.9	12.7 ± 2.8	9.0 ± 0.7	9.1 ± 0.8	8.6 ± 0.6	9.6 ± 1.9
	6.6 - 13.9	6.7 - 9.4	16.2 - 19.8	16.8 - 24.8	9.0 - 10.0	8.3 - 13.3	5.5 - 12.9	5.6 - 7.7	8.6 - 15.6	8.0 - 16.7	8.0 - 10.7	7.5 - 11.0	7.6 - 9.8	7.9 - 15.3
ESNOUT	11.7 ± 1.0	11.5 ± 0.9	27.4 ± 1.9	28.3 ± 3.7	13.7	14.1	9.4 ± 0.8	9.6 ± 0.5	19.4 ± 2.8	18.9 ± 4.3	12.9 ± 0.9	13.0 ± 1.0	12.3 ± 0.8	13.6 ± 2.5
	9.4 - 13.8	9.6 - 13.4	24.9 - 29.7	25.0 - 36.2	12.5 - 14.8	11.7 - 18.6	7.3 - 11.3	8.9 - 10.8	12.7 - 25.0	11.7 - 23.9	11.4 - 15.3	10.8 - 14.6	10.6 - 13.7	11.5 - 20.9
HUML	15.4 ± 2.3	14.2 ± 1.7	49.3 ± 2.5	48.8 ± 7.0	17.4	17.3	10.8 ± 1.6	9.9 ± 1.6	29.4 ± 5.8	27.2 ± 7.6	15.6 ± 2.1	15.4 ± 2.4	14.4 ± 1.0	15.2 ± 3.3
	11.0 - 19.5	10.5 - 16.7	44.8 - 51.7	42.2 - 62.8	16.7 - 18.0	16.0 - 19.5	8.2 - 14.1	7.7 - 14.4	17.7 - 37.7	13.7 - 38.5	11.3 - 19.8	10.0 - 20.2	12.0 - 16.8	10.5 - 23.8
RADL	11.5 ± 1.2	10.4 ± 1.2	34.2 ± 3.1	34.6 ± 4.3	13.0	13.3	9.4 ± 1.2	10.1 ± 1.2	21.6 ± 4.0	20.3 ± 5.8	12.4 ± 1.4	12.2 ± 1.4	10.9 ± 1.0	12.4 ± 2.1
	9.7 - 14.4	8.2 - 12.7	29.7 - 37.3	30.8 - 42.0	12.8 - 13.1	10.5 - 17.7	7.4 - 12.5	8.4 - 12.7	14.0 - 28.7	10.1 - 27.3	9.7 - 15.5	8.7 - 14.9	8.8 - 12.9	9.6 - 17.6
HNDL	11.3 ± 1.1	11.1 ± 1.0	38.5 ± 2.3	39.9 ± 5.1	15.0	16.2	9.7 ± 1.5	9.8 ± 1.2	24.0 ± 4.3	23.4 ± 6.1	13.6 ± 1.0	14.1 ± 1.0	13.0 ± 1.1	14.8 ± 3.0
	9.1 - 13.9	9.4 - 13.1	36.1 - 42.5	36.1 - 51.0	14.8 - 15.2	14.6 - 19.0	6.3 - 12.9	7.8 - 12.2	15.2 - 31.0	12.9 - 33.7	11.6 - 16.3	12.3 - 17.3	10.6 - 14.9	12.0 - 24.0
FG3L	6.3 ± 0.7	6.4 ± 0.9	25.1 ± 1.6	24.5 ± 3.1	9.4	10.9	5.7 ± 0.9	5.9 ± 1.0	14.6 ± 3.0	14.6 ± 4.3	8.8 ± 1.3	9.0 ± 0.9	8.3 ± 1.1	9.6 ± 2.6
	5.0 - 8.0	5.0 - 8.3	23.2 - 27.6	21.4 - 30.4	9.4 - 9.4	9.4 - 13.9	4.2 - 7.6	3.8 - 8.1	7.7 - 18.9	6.0 - 21.1	6.9 - 11.3	7.3 - 10.6	6.0 - 10.6	7.0 - 18.0
FEML	25.5 ± 3.4	24.3 ± 3.2	62.3 ± 2.7	63.5 ± 4.0	25.2	28.4	19.5 ± 2.0	20.6 ± 1.4	43.2 ± 7.8	39.8 ± 10.5	24.8 ± 2.4	24.6 ± 3.1	23.8 ± 1.5	27.0 ± 4.7
	20.4 - 34.8	19.5 - 32.7	59.5 - 66.3	57.8 - 68.9	24.4 - 25.9	25.0 - 31.5	14.4 - 24.2	16.7 - 23.3	26.8 - 53.6	18.3 - 52.4	18.7 - 29.0	18.0 - 31.3	20.1 - 28.0	21.0 - 37.4
TIBL	23.6 ± 2.8	22.8 ± 2.6	56.4 ± 4.5	59.2 ± 6.5	27.3	28.1	20.3 ± 2.2	20.9 ± 1.8	44.5 ± 8.0	41.4 ± 10.9	24.5 ± 1.5	24.2 ± 1.6	25.1 ± 1.5	27.6 ± 4.3
	18.6 - 30.3	18.9 - 29.4	50.9 - 62.5	53.4 - 73.0	25.8 - 28.8	24.1 - 35.0	16.4 - 24.5	18.0 - 25.6	27.1 - 56.8	20.4 - 57.5	21.4 - 26.8	20.5 - 27.0	21.0 - 28.3	21.4 - 36.8
FOOTL	36.1 ± 4.4	36.5 ± 3.9	92.5 ± 4.6	98.1 ± 6.7	41.3	44.6	31.6 ± 3.8	32.9 ± 3.0	71.0 ± 12.9	67.2 ± 17.1	37.9 ± 3.0	37.9 ± 3.5	38.1 ± 2.8	43.8 ± 7.0
	31.0 - 49.4	30.2 - 45.1	86.1 - 98.3	91.0 - 112.3	40.3 - 42.2	38.3 - 53.7	25.5 - 40.5	29.3 - 41.0	46.2 - 86.4	35.3 - 90.0	29.0 - 42.3	25.0 - 42.2	32.8 - 42.7	37.2 - 62.4
TOE1L	4.9 ± 0.6	5.1 ± 0.6	15.9 ± 1.6	17.5 ± 2.4	6.4	6.6	4.4 ± 0.5	5.0 ± 0.7	10.2 ± 2.2	9.8 ± 3.0	4.9 ± 0.5	4.8 ± 0.7	5.8 ± 0.6	6.8 ± 1.2
	3.9 - 6.7	3.7 - 6.5	13.6 - 18.3	15.2 - 22.6	5.4 - 7.3	5.5 - 8.6	3.6 - 5.5	3.7 - 6.0	5.8 - 13.4	5.0 - 14.4	3.9 - 5.8	3.7 - 5.9	4.3 - 6.7	5.4 - 10.3
TOE4L	24.0 ± 2.7	23.4 ± 2.3	58.8 ± 2.9	60.8 ± 3.2	27.3	29.2	20.6 ± 2.3	22.0 ± 1.9	47.7 ± 8.8	45.6 ± 12.1	24.4 ± 2.2	25.1 ± 2.8	25.8 ± 2.2	29.9 ± 4.9
	20.6 - 29.5	19.4 - 28.7	55.6 - 62.9	56.0 - 65.2	25.5 - 29.0	26.5 - 33.6	17.6 - 26.5	19.4 - 26.7	29.2 - 57.7	25.1 - 67.7	16.7 - 28.0	13.6 - 29.0	21.1 - 28.6	24.4 - 41.7
CIL	2.3 ± 0.5	2.3 ± 0.5	4.6 ± 0.7	4.5 ± 0.9	3.6	3.4	2.2 ± 0.4	2.2 ± 0.3	4.5 ± 1.0	4.3 ± 1.2	2.4 ± 0.6	2.7 ± 0.6	2.6 ± 0.3	2.9 ± 0.6
	1.6 - 3.5	1.6 - 3.8	3.7 - 5.2	3.4 - 5.5	3.3 - 3.8	3.2 - 3.6	1.4 - 2.8	1.7 - 3.1	2.7 - 6.5	2.6 - 6.5	1.1 - 3.2	1.5 - 4.3	2.0 - 3.1	2.1 - 4.4
WEBL	7.4 ± 1.5	6.9 ± 1.4	29.2 ± 3.7	27.1 ± 3.9	7.6	5.0	6.8 ± 1.7	7.8 ± 1.0	19.1 ± 4.4	18.1 ± 6.5	9.8 ± 3.8	10.4 ± 3.8	9.7 ± 4.5	10.6 ± 5.5
	4.2 - 11.3	4.2 - 9.6	24.5 - 34.6	22.2 - 34.5	4.2 - 10.9	3.2 - 8.3	3.9 - 10.0	6.2 - 10.1	9.5 - 25.2	7.3 - 27.4	4.4 - 16.0	4.0 - 17.5	3.8 - 17.8	5.4 - 23.3

Table II - Ratios of morphometric data for *Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris*, *T. carrillae*, *T. culeus*, *T. jelskii* and *T. rimac*. Data are given as mean ± 1 SD. See text for abbreviations of variables.

Ratio	*B. brachydactylus*	*B. macrostomus*	*T. brevirostris*	*T. carrillae*	*T. culeus*	*T. jelskii*	*T. rimac*
	N = 53	N = 13	N = 5	N = 53	N = 42	N = 72	N = 42
BH/SVL	0.194 ± 0.047	0.176 ± 0.025	0.285 ± 0.023	0.231 ± 0.020	0.292 ± 0.032	0.252 ± 0.028	0.240 ± 0.029
HWID/SVL	0.314 ± 0.026	0.404 ± 0.024	0.347 ± 0.034	0.302 ± 0.021	0.397 ± 0.037	0.364 ± 0.026	0.337 ± 0.026
EYE/SVL	0.085 ± 0.014	0.060 ± 0.007	0.103 ± 0.004	0.085 ± 0.012	0.076 ± 0.009	0.100 ± 0.015	0.106 ± 0.012
IOD/SVL	0.240 ± 0.021	0.238 ± 0.010	0.281 ± 0.011	0.242 ± 0.019	0.240 ± 0.014	0.270 ± 0.026	0.282 ± 0.022
ENOSE/SVL	0.151 ± 0.015	0.143 ± 0.005	0.167 ± 0.006	0.152 ± 0.022	0.138 ± 0.012	0.167 ± 0.014	0.170 ± 0.013
ESNOUT/SVL	0.206 ± 0.016	0.212 ± 0.007	0.236 ± 0.013	0.210 ± 0.014	0.211 ± 0.018	0.238 ± 0.015	0.243 ± 0.016
HUML/SVL	0.262 ± 0.034	0.373 ± 0.020	0.299 ± 0.027	0.233 ± 0.037	0.306 ± 0.025	0.285 ± 0.043	0.280 ± 0.028
RADL/SVL	0.195 ± 0.022	0.262 ± 0.017	0.227 ± 0.014	0.215 ± 0.017	0.227 ± 0.015	0.226 ± 0.023	0.218 ± 0.021
HNDL/SVL	0.199 ± 0.021	0.299 ± 0.017	0.270 ± 0.020	0.217 ± 0.027	0.257 ± 0.017	0.255 ± 0.023	0.260 ± 0.022
FG3L/SVL	0.113 ± 0.015	0.189 ± 0.017	0.176 ± 0.012	0.128 ± 0.017	0.158 ± 0.019	0.163 ± 0.025	0.166 ± 0.024
FEML/SVL	0.440 ± 0.038	0.481 ± 0.039	0.468 ± 0.062	0.445 ± 0.037	0.452 ± 0.032	0.453 ± 0.043	0.475 ± 0.039
TIBL/SVL	0.410 ± 0.035	0.441 ± 0.019	0.475 ± 0.021	0.457 ± 0.027	0.467 ± 0.034	0.448 ± 0.033	0.495 ± 0.037
FOOTL/SVL	0.640 ± 0.047	0.729 ± 0.039	0.741 ± 0.051	0.713 ± 0.042	0.751 ± 0.062	0.695 ± 0.070	0.763 ± 0.044
TOE1L/SVL	0.088 ± 0.010	0.127 ± 0.010	0.110 ± 0.011	0.104 ± 0.013	0.108 ± 0.013	0.089 ± 0.011	0.117 ± 0.012
TOE4L/SVL	0.418 ± 0.030	0.458 ± 0.033	0.489 ± 0.047	0.469 ± 0.029	0.506 ± 0.042	0.454 ± 0.041	0.519 ± 0.047
CIL/SVL	0.041 ± 0.009	0.035 ± 0.006	0.060 ± 0.009	0.049 ± 0.006	0.047 ± 0.007	0.047 ± 0.011	0.051 ± 0.008
WEBL/SVL	0.126 ± 0.026	0.214 ± 0.027	0.101 ± 0.053	0.159 ± 0.027	0.198 ± 0.036	0.187 ± 0.072	0.191 ± 0.087
CIL/TOE1L	0.472 ± 0.107	0.275 ± 0.050	0.555 ± 0.123	0.484 ± 0.092	0.440 ± 0.066	0.536 ± 0.144	0.442 ± 0.056
FEML/TIBL	1.072 ± 0.074	1.092 ± 0.084	1.002 ± 0.090	0.975 ± 0.075	0.972 ± 0.074	1.013 ± 0.080	0.960 ± 0.058

functions were derived from the log_{10}-transformed data and from the ratios. The degree of separation of taxa was almost identical in both analyses and therefore we present the results using the log_{10}-transformed data only (analogous to WIENS, 1993).

All calculations were performed on a PC using the FORTRAN77 program CLUSTER and the program package STATGRAPHICS, version 5 5.

RESULTS

INTRASPECIFIC VARIATION

Among the seven nominal species studied in this paper, four are thought to segregate in subspecies: *Telmatobius brevirostris*, *T. culeus*, *T jelskii* and *T. rimac* (VELLARD, 1951, 1953, 1955). We approached the problem of morphometric variation within a nominal species by applying cluster analysis on the phenotypes of all conspecific individuals available, including those which VELLARD assigned as type material for the proposed subspecies. Phenotypes are described by 19 SVL-standardized morphometric ratios to minimize size effects.

The phenograms of all species (including those without subspecific segregation) revealed existence of different intraspecific morphological traits documented by groups of specimens which joined to the same cluster with an error sum of squares of less than 0.1 (figs. 3-6, data on *Batrachophrynus* and *T. carrillae* not shown). We treat these groups of remarkably similar specimens as "morphs", without intending a taxonomic implication. Generally, intraspecific morphs did not reflect polymorphism related to sex or size.

Telmatobius brevirostris *Vellard, 1955*

VELLARD (1955) recognized three subspecies: *Telmatobius b. brevirostris*, *T. b. parvulus* and *T. b. punctatus*. Unfortunately, we only found in the MHNSM collection two specimens of the first two subspecies, and one of the third. The original descriptions were based on only three adults of *T. b. brevirostris*, six of *T b parvulus* and two of *T. b. punctatus* – a prohibitively small sample size to define reliable subspecific taxa. The phenogram (fig. 3) of the five specimens available for analysis shows that: (1) the two type specimens of *T. b. brevirostris* from Chasqui join different clusters; (2) the morphometrically most similar specimens are one *T b brevirostris* individual and the *T. b. punctatus* male from Santa Maria del Valle; (3) the two individuals of *T b. parvulus* from Caina are very alike, but form together with one *T. b. brevirostris* a main cluster with a error sum of squares far below the level of morph distinction. All specimens join to one group at an error sum of squares of only 0.146. Neither the association of the five phenotypes to groups nor the degree of morphological differentiation between them support a subspecific segregation within the nominal species *T. brevirostris*.

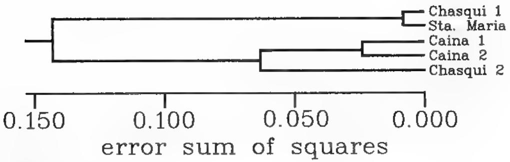


FIG. 3 — Phenogram of morphometric similarity between adult *Telmatobius brevirostris* which VELLARD (1955) assigned to different subspecies. Each specimen is identified by the locality of collection and an individual number. Similarity is based on 19 ratios and computed by hierarchical grouping in a cluster analyis. *T. b. brevirostris*: Chasqui, *T. b. parvulus*: Caina, *T. b. punctatus*: Santa Maria del Valle.

Telmatobius culeus *(Garman, 1875)*

VELLARD (1953) recognized six subspecies: *Telmatobius c. culeus*, *T. c. dispar* (redescribed by LAVILLA, 1988b), *T. c. escomeli*, *T. c. exsul*, *T. c. fluviatilis* and *T. c. lacustris*. The phenogram (fig. 4) calculated for 42 adults assigned as type material (MHNSM) reveals that: (1) there exist five morphs within the nominal species; (2) these morphs do not coincide with any of the subspecies proposed by VELLARD; (3) different morphs occur at the same locality. Joining all specimens to one group causes an error sum of square of 0.453, that is three times greater than in *T. brevirostris*. Again, from the morphometric point of view there is no evidence that the morphological traits within *T. culeus* agree with the proposed subspecific differentiation.

Telmatobius jelskii *(Peters, 1873)*

VELLARD (1955) recognized four subspecies. *Telmatobius j. jelskii*, *T. j. bufo* (redescribed by LAVILLA, 1988b), *T. j. longitarsis* and *T. j. walkeri*. The phenogram (fig. 5) of 72 adults including VELLARD's type specimens (MHNSM) shows that: (1) there exist seven morphs within the nominal species; (2) these morphs do not coincide with any of the subspecies proposed by VELLARD; (3) different morphs inhabit the same locality. Joining all specimens to one group causes an error sum of squares of 1.444, that is three times greater than in *T. culeus* or in *T. rimac* and ten times greater than in *T. brevirostris*. Nevertheless, the occurrence of different morphs at all sites — though in different frequencies — does not support the validity of the four subspecies proposed by VELLARD.

Telmatobius rimac *Schmidt, 1954*

VELLARD (1955) recognized two subspecies: *Telmatobius r. rimac* and *T. r. meridionalis*. The phenogram (fig. 6) of 42 adults including VELLARD's type specimens shows that: (1) there are five morphs; (2) the type material from Ocros and Tupe forms one of two

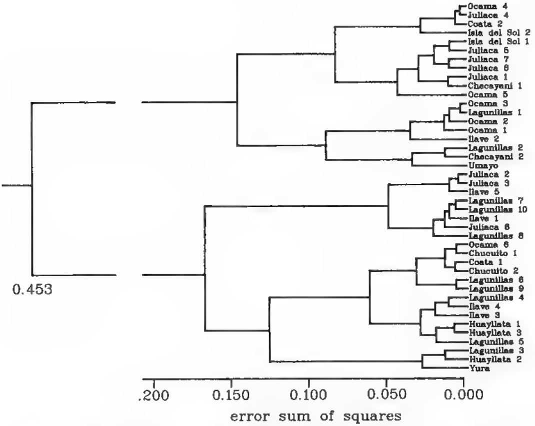


Fig 4 – Phenogram of morphometric similarity between adult *Telmatobius culeus* which Vellard (1953) assigned to different subspecies. Presentation of data analogous to that in fig. 3. *T. c. culeus*: Ocama, Ilave, Isla del Sol, *T. c. dispar*: Coata, Juliaca; *T. c. escomeli*: Lagunillas; *T. c. exsul*: Yura; *T. c. fluviatilis*: Chucuito, Huayllata, Ilave; *T. c. lacustris*. Checayani, Umayo

main clusters including two mixed morphs; (3) the more recently collected material from Obrojillo and Huaytara (situated at the same distance to Ocros in the north and to Tupe in the south) forms the second main cluster and segregates into three more morphs; (4) only one individual (Obrojillo 3) directly joins the cluster of the type specimens. This unexpected structure of the phenogram does not support the validity of the proposed subspecies, but demonstrates suspicious differences between the external morphology of *T. rimac* which were collected forty years ago and those presently inhabiting the streams of the Pacific slope of the Andes.

Interspecific variation

In order to compare the intraspecific variation with the morphometric differences among the nominal species, we performed principal component analysis and discriminant analysis on two groups of geographically neighbouring species: (1) the northern Tel-

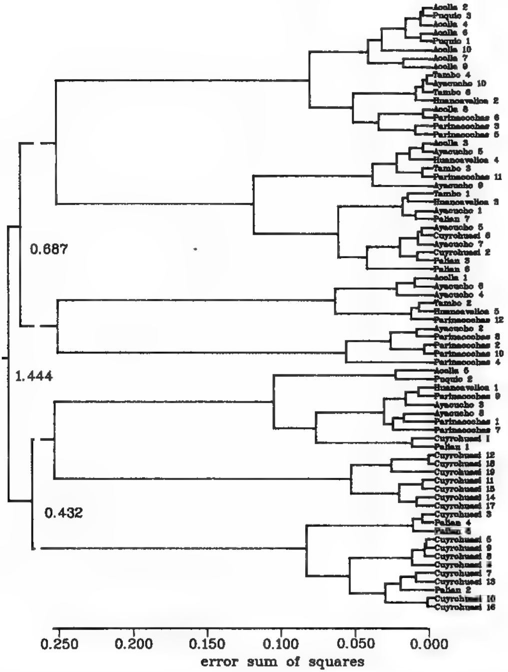


Fig. 5 Phenogram of morphometric similarity between adult *Telmatobius jelskii* which VELLARD (1955) assigned to different subspecies. Presentation of data analogous to that in fig. 3. *T. j. jelskii*: Acolla; *T. j. bufo*: Tambo; *T. j. longitarsis*: Huancavelica, Puquio; *T. j. walkeri*: Ayacucho. Unclassified *T. jelskii* were collected in Palian, Cuyrohuasi and Parinacochas

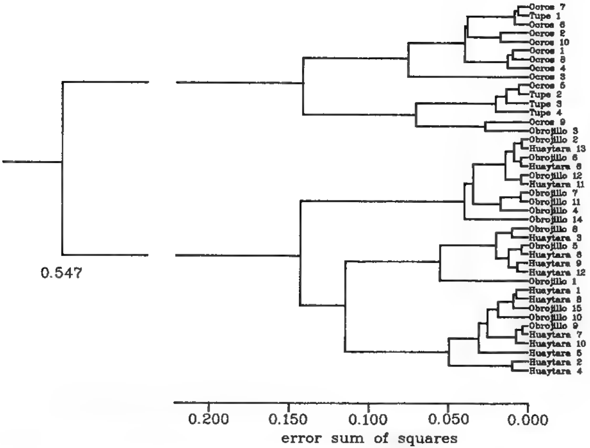


Fig. 6. – Phenogram of morphometric similarity between adult *Telmatobius rimac* which VELLARD (1955) assigned to different subspecies. Presentation of data analogous to that in fig. 3. *T. r. rimac*: Ocros, *T. r. meridionalis*: Tupe. Unclassified *T. rimac* were collected in Obrojillo and Huaytara.

matobiinae including *Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris* and *T. carrillae*; (2) the southern *Telmatobius* species *T. culeus*, *T. jelskii* and *T. rimac*. The main reason for the subdivision of the complete data set on phenotypes into groups of three and four species, respectively, was to reduce the number of significant canonical variables to two, which permits the distinction of these taxa in two-dimensional scatter plots (figs. 7-8). Here, we present only the results based on $\log_{10}$-transformed data because the separation of taxa by discriminant analysis was almost identical in data sets of 18 $\log_{10}$-transformed distances and in those consisting of 19 morphometric ratios.

Generally, the interspecific differences in size (PC1) by far exceeded those in shape (PC2, PC3). The size effects on PC2 and PC3 appeared to be small, because shearing did not notably improve the separation of taxa. Discriminant analysis led to an almost optimal separation of species by combining differences in size and shape.

In the northern group of central Peruvian Telmatobiinae, the first three principal components explained 95.0 % of the total variance. PC1 distinguishes the large *B. macrostomus* from the smaller three species. The plot of PC2 and PC3 scores (fig. 7A) shows a wide overlap between *B. macrostomus*, *B. brachydactylus* and *T. carrillae*, whereas PC3 distinguishes four of the five *T. brevirostris* from the other species. An almost complete separation of the four taxa was obtained by discriminant analysis, only 2 out of 53 *B. brachydactylus* were confounded with *T. carrillae* (fig. 7B, Table III). The separation of taxa is mainly based on size (SVL) and interorbital distance (IOD) in CAN1, and on size (SVL), head shape (HWID, EYE, IOD) and humerus length (HUML) in CAN2.

In the southern group of *Telmatobius* species the first three principal components accounted for 92.9 % of the total variance. PC1 distinguishes *T. culeus* from the other two species. The plot of principal component scores (fig. 8A) shows a considerable separation of *T. jelskii* from *T. rimac* based on PC3, but a complete overlap of *T. culeus* with both other species. An almost complete separation of the three taxa was obtained by canonical discriminant analysis, only 1 out of 42 *T. culeus* was confounded with *T. jelskii*, and 1 out of 72 *T. jelskii* with *T. rimac* (fig. 8B, Table IV). The separation of species is mainly based on size (SVL, BH) and head shape (ENOSE, ESNOUT) in CAN1, and on size (SVL), head shape (HWID, ESNOUT) and extremity length (HANDL, TIBL) in CAN2.

INTERGENERIC VARIATION

The next step of analysis concerns the morphometric features of each genus and the possibility to identify genus-specific morphometric characters or ratios. The data of the two *Batrachophrynus* species form one group, those of the five *Telmatobius* taxa the other. Again, $\log_{10}$-tranformed data and ratios provided the same degree of group separation. A highly significant discriminant function was obtained which correctly classifies 80 % of the *Batrachophrynus* and 96 % of the *Telmatobius* ($\log_{10}$-transformed data, Table V). Distinctive morphometric ratios (ANOVA, $P < 0.01$) were BH/SVL (fig. 9A) and FEML/TIBL (fig. 9B).

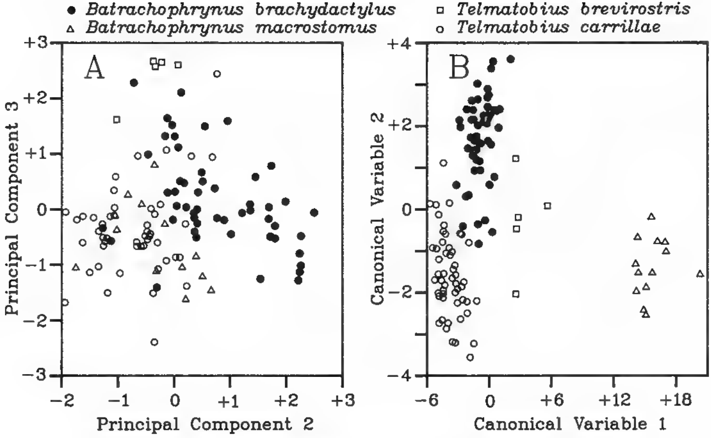


Fig. 7. Plot of (A) principal component scores and (B) discriminant function scores of the four northern telmatobiine species: *Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris* and *T. carrillae*. Discriminant functions and classification success are given in Table III.

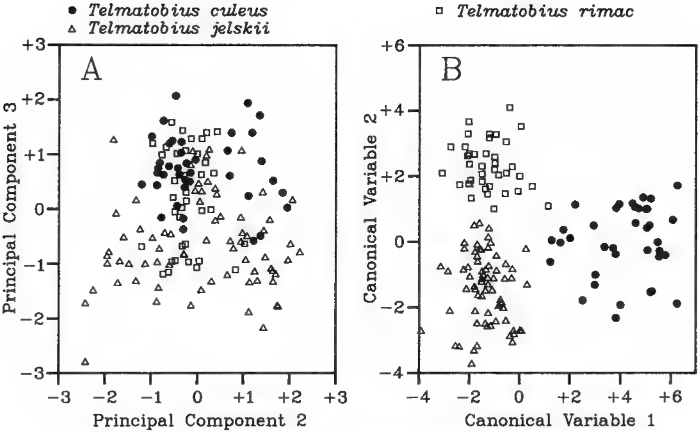


Fig. 8 — Plot of (A) principal component scores and (B) discriminant function scores of the three southern telmatobiine species *Telmatobius jelskii*, *T. rimac* and *T. culeus*. Discriminant functions and classification success are given in Table IV.

Table III. - Discriminant functions to distinguish among *Batrachophrynus macrostomus*, *B. brachydactylus*, *Telmatobius brevirostris* and *T. carrillae* based on 18 $\log_{10}$ transformed morphometric characters.

A. Statistical significance

Eigenvalue	Canonical correlation	Wilks Lambda	Chi-squared	Degrees of freedom	P
32.10	0.985	0.0042	613.5	54	< 0.00001
3.43	0.842	0.1383	221.5	34	< 0.00001
1.11	0.725	0.4741	583.6	16	< 0.00001

B. Unstandardized discriminant function coefficients

Character	Coefficients		
	CAN 1	CAN 2	CAN 3
SVL	- 11.64	18.89	- 6.59
BH	- 3.60	- 0.10	4.81
HWID	2.91	17.56	- 9.19
EYE	- 6.78	10.25	2.81
IOD	25.39	- 12.21	14.51
ENOSE	- 4.42	- 4.49	- 10.26
ESNOUT	6.79	- 7.75	7.84
HUML	1.64	11.01	0.92
RADL	5.77	- 7.09	- 3.67
HNDL	6.99	- 5.13	- 1.41
FG3L	6.92	- 1.94	6.82
FEML	9.23	6.85	- 4.27
TIBL	- 5.42	- 8.20	6.23
FOOTL	- 8.38	1.21	- 4.85
TOE1L	4.57	- 7.16	1.60
TOE4L	2.50	- 8.12	7.13
CIL	- 2.14	- 0.50	3.27
WEBL	- 1.62	- 3.84	- 9.81
Constant	- 25.08	- 13.17	0.75

C. Classification success

Actual group	Predicted group			
	Batrachophrynus brachydactylus	*Batrachophrynus macrostomus*	*Telmatobius brevirostris*	*Telmatobius carrillae*
B. brachydactylus	51 (96%)	0	0	2 (4%)
B. macrostomus	0	13 (100%)	0	0
T. brevirostris	0	0	5 (100%)	0
T. carrillae	0	0	0	53 (100%)

D. Group centroids

Species	CAN 1	CAN 2	CAN 3
B. brachydactylus	- 0.71	1.75	- 0.16
B. macrostomus	15.59	- 0.98	- 0.58
T. brevirostris	- 3.41	- 1.49	- 0.17
T. carrillae	3.17	- 0.24	5.02

Table IV. - Discriminant functions to distinguish among *Telmatobius culeus*, *T. jelskii* and *T. rimac* based on 18 $\log_{10}$ transformed morphometric characters.

A. Statistical significance

Eigenvalue	Canonical correlation	Wilks Lambda	Chi-squared	Degrees of freedom	P
5 47	0.919	0.0416	440.3	36	< 0.00001
2 71	0.855	0.2694	181.7	17	< 0.00001

B Unstandardized discriminant function coefficients

Character	Coefficients	
	CAN 1	CAN 2
SVL	9.53	10 88
BH	11.13	- 0.17
HWID	9.72	- 16.42
EYE	- 5.73	3.52
IOD	6 65	9 22
ENOSE	- 23.94	0.08
ESNOUT	11.85	11.20
HUML	7.22	- 8.12
RADL	- 3.76	- 6.35
HNDL	3.47	- 10.22
FG3L	- 6.56	- 4.35
FEML	8.74	- 0.34
TIBL	3.17	15.38
FOOTL	9.28	0.19
TOE1L	2.54	15.19
TOE4L	7.25	9.55
CIL	1.88	1.25
WEBL	0.55	- 0 48
Constant	- 10.60	1 19

C. Classification success

Actual group	Predicted group		
	Telmatobius culeus	*Telmatobius jelskii*	*Telmatobius rimac*
Telmatobius culeus	41 (98%)	1 (2%)	0
Telmatobius jelskii	0	71 (99%)	1 (1%)
Telmatobius rimac	0	0	42 (100%)

D. Group centroids

Species	CAN 1	CAN 2
Telmatobius culeus	4.05	- 0 06
Telmatobius jelskii	- 1.37	- 1.42
Telmatobius rimac	- 1.25	2 46

Table V. Discriminant functions to distinguish the genera *Batrachophrynus* and *Telmatobius* based on 18 log_{10} transformed morphometric characters.

A. Statistical significance

Eigenvalue	Canonical correlation	Wilks Lambda	Chi-squared	Degrees of freedom	P
1.63	0.788	0.3794	254.9	18	< 0.00001

B. Unstandardized discriminant function coefficients

Character	Coefficients
	CAN 1
SVL	- 19.89
BH	8.83
HWID	0.90
EYE	- 0.77
IOD	- 3.75
ENOSE	- 10.09
ESNOUT	11.96
HUML	- 5.36
RADL	- 0.61
HNDL	6.05
FG3L	4.03
FEML	- 9.71
TIBL	13.01
FOOTL	- 3.93
TOE1L	- 2.39
TOE4L	10.08
CIL	- 0.23
WEBL	0.56
Constant	13.78

C. Classification success

Actual group	Predicted group	
	Batrachophrynus	*Telmatobius*
Batrachophrynus	53 (80%)	13 (20%)
Telmatobius	8 (4%)	200 (96%)

D. Group centroids

Genus	CAN 1
Batrachophrynus	- 2 26
Telmatobius	0.72

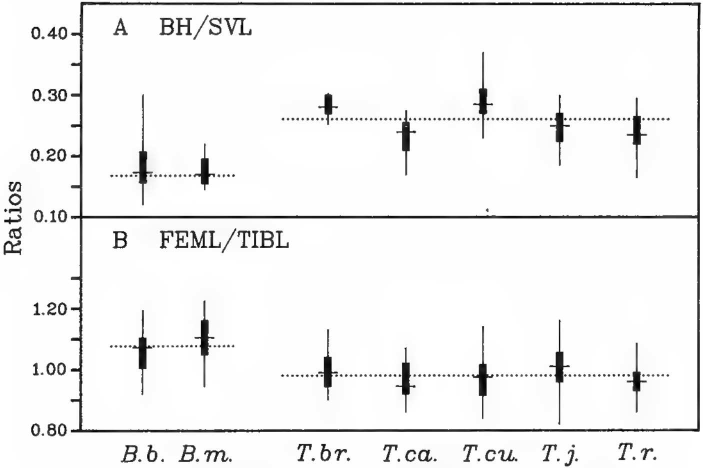


Fig. 9 – Box- and whisker-plot of morphometric ratios which permit the distinction between the genera *Batrachophrynus* and *Telmatobius* (A) BH/SVL; (B) FEML/TIBL. The dotted line represents the means of each genus. B.b.: *Batrachophrynus brachydactylus*; B.m.: *B. macrostomus*; T.b.: *Telmatobius brevirostris*; T.ca.: *T. carrillae*; T.cu.: *T. culeus*, T.j.: *T. jelskii*; T.r.: *T. rimac*.

Variation between ecotypes

Finally, we examined the relationship of morphological traits caused by the convergent adaptation to a specific type of habitat (stream/lake) with the phylogenetic relationships between the seven taxa. For this purpose, we pooled the data of *B. macrostomus* and *T. culeus* forming the lake group and compared them with the stream group formed by the remaining species. Again, there was no difference between the separation of groups based on log_{10}-transformed data and that based on ratios. The highly significant discriminant function correctly classifies 100 % of the stream-inhabitants and 92 % of the lake-inhabitants (log_{10}-transformed data, Table VI). Distinctive morphometric ratios (ANOVA, $P < 0.01$) between lake- and stream-inhabitants are HWID/SVL (fig 10A) and EYE/SVL (fig. 10B). Moreover, SVL of adult lake-inhabitants is considerably larger than that of stream-inhabitants (Table I).

Discussion

The general similarity in size and shape of the riparian central Peruvian Telmatobiinae does not facilitate a reliable and objective definition of taxa. Trueb (1979) stated that most taxonomic descriptions of *Telmatobius* are inadequate because many proposed diagnostic characters are so subjective that an identification without comparison with type material is almost impossible. A recent study on the *Telmatobius* species of northern Perú used for the first time multivariate statistics on morphometric data to obtain objective criteria for the classification of telmatobiine frogs (Wiens, 1993). We followed this approach and successfully applied cluster, principal component and discriminant analyses to assess the morphometric variation within and among the central Peruvian taxa of Telmatobiinae. Consequently, we offer discriminant functions based on external characters which permit the identification of adults with a very low rate of erroneous classifications. Moreover, we identified convergent morphological traits distinguishing riparian and lake-inhabiting telmatobiine frogs which in the future should be avoided for taxonomic conclusions.

Reassessment of the subspecific taxa

Within wide ranging species such as *T. jelskii* and *T. rimac* we are confronted with the problem of interpopulational morphological differentiation, due to the partial geographical isolation between different hydrographic systems and valleys. Vellard (1951, 1953, 1955) attempted to solve this problem by naming more than half of the populations studied up to 1955 at the subspecific level. However, the existence of a complete series of intermediate specimens (Vellard, 1955) between all subspecies emphasizes the more or less arbitrary nature of their definition. Nevertheless, due to Vellard's proposal, the segregation of *T brevirostris*, *T. culeus*, *T jelskii* and *T. rimac* into a total of fifteen (!) subspecies is still recognized (Frost, 1985).

Our attempt to deal with interpopulational variability in taxonomic terms is based on the hierarchical grouping of individual phenotypes according to their similarity in external

Table VI. - Discriminant function to distinguish between the stream- and lake-inhabiting species of the genera *Batrachophrynus* and *Telmatobius* based on 18 log_{10} transformed morphometric characters.

A. Statistical significance

Eigenvalue	Canonical correlation	Wilks Lambda	Chi-squared	Degrees of freedom	P
4.58	0.906	0.1792	452.1	18	< 0 00001

B. Unstandardized discriminant function coefficients

Character	Coefficients
	CAN 1
SVL	3.21
BH	4.72
HWID	8.12
EYE	- 4.01
IOD	- 5.74
ENOSE	- 8.33
ESNOUT	0.77
HUML	6.98
RADL	- 1.30
HNDL	4.85
FG3L	- 6 24
FEML	- 3.29
TIBL	- 3.84
FOOTL	7.42
TOE1L	3.14
TOE4L	7.58
CIL	0 24
WEBL	0.87
Constant	16.34

C. Classification success

Actual group	Predicted group	
	Stream-inhabitant	Lake-inhabitant
Stream-inhabitant	224 (100%)	0
Lake-inhabitant	4 (8%)	46 (92%)

D. Group centroids

Genus	CAN 1
Stream-inhabitant	- 1.01
Lake-inhabitant	4.51

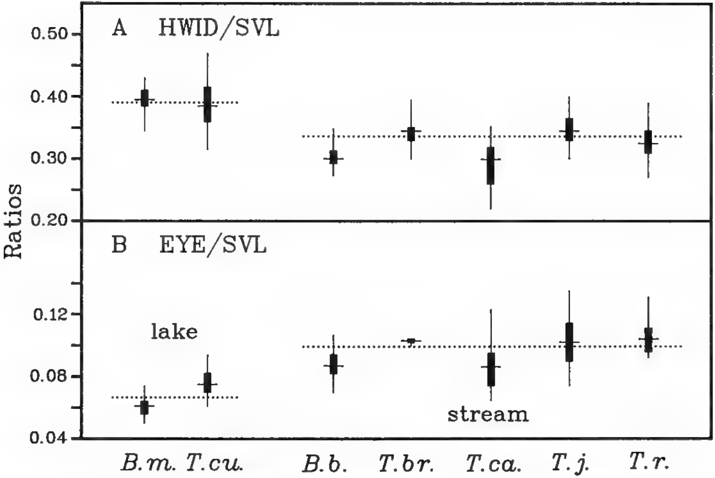


Fig 10 – Box- and whisker-plot of morphometric ratios which permit the distinction between inhabitants of lakes and of streams (A) HWID/SVL; (B) EYE/SVL. Presentation of data analogous to fig. 9.

morphology To avoid major biasses due to size, the phenotypes are described by 19 unweighted morphometric ratios. The phenotypic grouping in a cluster analysis permits an objective assessment of similarity between conspecific individuals, even if the sample size is small as usually for type material. Principal component and discriminant analyses, in contrast, require about 20 cases per predictor which imply sample sizes exceeding by far the numbers of type specimens.

VELLARD's proposal of subspecies is exclusively based on differences in the external morphology of specimens from different localities. Therefore, if the proposed subspecies were valid, the phenograms of conspecific individuals collected from different localities (= reproductively isolated populations) should show the following structure: (1) specimens pertaining to the material originating from one type locality should form a homogeneous group (cluster); (2) material assigned to different subspecies should be represented in different clusters; (3) conspecific specimens originating from one population without their own subspecific status should join as a group one cluster formed by type specimens.

The phenograms obtained for *T. brevirostris*, *T. culeus*, *T jelskii* and *T. rimac* do not show structures compatible with VELLARD's taxonomic suggestions. The morphometric differentiation between the five specimens of *T. brevirostris* which VELLARD assigned to three subspecies is low and the most similar pair of individuals belongs to different subspecies (fig. 3). The greatest morphometric difference between the 42 *T. culeus* exceeds three times that between the *T. brevirostris* specimens but none of the five morphs identified within this data set coincides with any of the proposed subspecies (fig. 4). The same applies to the seven and five morphs, respectively, found within the *T. jelskii* (fig. 5) and *T. rimac* (fig. 6) data sets. As objective morphometric similarity does not correspond to VELLARD's subjective grouping of conspecific specimens to subspecies, we conclude that the proposed subspecific segregation is invalid in the four species studied This conclusion does not rule out that the definition of subspecies may be useful to describe the speciation processes due to the geographic isolation of populations of wide ranging species. However, if considered useful, the definition should be based on conceivable, objective criteria better than those presented so far.

What is the meaning of the different morphological traits (morphs = groups of conspecific specimens which are morphometrically very similar) which we detected in all seven species? As different morphs usually occur at the same locality, i.e. within the same population, they probably do not represent taxonomically relevant units. Neither do they reflect sexual dimorphism in shape, or size-specific polymorphism. The varying frequencies of morphs at different localities indicate that the adaptive value of a morph for the increase of individual fitness probably differs among the localities. Thus, intraspecific polymorphism may have evolved in response to local environmental factors such as altitude, water flow and competition. The occurrence of different morphs at the same locality may be due to temporal changes in the local environments. This interpretation is supported by the conspicuous change of the frequencies of *T. jelskii* morphs which took place in the Mantaro Valley during the last forty years 9 out of 10 specimens collected near Acolla in the early fifties (VELLARD, 1955), but only 1 out of 7 frogs recently collected near Palian join the same main cluster, whereas only 1 Acolla specimen joins the remaining 6 Palian specimens. Even more impressive is the same tendency in *T. rimac* though

referring to geographically distant localities: only one recently collected individual pertains to the morphs dominating about forty years before (Vellard, 1955). Attributing these changes to the different duration of preservation seems too simple because older morphs still occur (rarely) in contemporary populations, and presently dominating morphs also existed (rarely) forty years ago. Instead, there have been dramatic changes in the riparian habitats of these species during this period due to the enormous increase in human population and the resulting pollution of the rivers and streams.

In summary, we reject the proposal of subspecies for *T. brevirostris*, *T. culeus*, *T. jelskii* and *T. rimac*.

Reassessment of the species status

The large numbers of studied specimens in most species permit a reliable estimate of the intraspecific morphometric variability and the comparison between different species. Principal component analysis of the $\log_{10}$-transformed data did not substantially contribute to the resolution between different taxa: the usually large overlap between different species reflects their similarity in many aspects of shape. The only exception from the rule is *T. brevirostris* which considerably differs from the neighbouring species (fig. 7A). However, Wiens (1993) obtained a similar low degree of resolution between eight *Telmatobius* species from northern Perú, indicating that PCA is not a powerful tool to distinguish between Andean Telmatobiinae.

In contrast, if groups (= species) are determined a priori, and if the differences between them are maximized by canonical discriminant analysis, the same morphometric data sets can distinguish between the taxa. It is noteworthy that, despite the bad image of morphometric ratios (e.g. Bookstein et al., 1985), discriminant analysis using $\log_{10}$-transformed data or ratios give very similar results and reach the same classification success. The convergent morphological adaptation to similar environmental constraints prevents an unequivocal identification at the level of individuals, but the rate of erroneously classified individuals is low: 2 *B. brachydactylus*, 1 *T. culeus* and 1 *T. jelskii* out of a total of 280 specimens. Wiens (1993) did not provide results of classification success in his analysis, but he also stated that discriminant analysis provided an objective base for the distinction between Andean species of Telmatobiinae. In summary, the six central Peruvian species as well as the one from southern Perú proved to be well-defined taxonomic units which possess external features allowing an objective diagnosis.

Reassessment of the generic status

Laurent (1983) recognized three genera within the central Peruvian Telmatobiinae: the monotypic genera *Batrachophrynus* and *Lynchophrys*, and *Telmatobius* with four species. However, the evidence presented for the change of *Batrachophrynus brachydactylus* to the genus *Lynchophrys* is weak. the main differences from *Batrachophrynus macrostomus* put forward are: (1) shorter third finger; (2) smaller size; (3) the statement that male *B. macrostomus* lack nuptial pads. Points (1) and (2) are convergent morphological adaptations to the stream habitat which are shared with all riparian *Telmatobius*, whereas point (3) is simply an error (see figure 16 in Sinsch, 1990). Moreover, both species share two morphometric features which are diagnostic for the genus *Batrachophrynus* despite

their adaptation to different habitats: flat body and femur length exceeding tibia length Finally, the analysis of allozymes of these species and of three *Telmatobius* species (SINSCH & JURASKE, 1995) clearly demonstrates that *B. brachydactylus* and *B. macrostomus* are closely related species as originally proposed by PETERS (1873).

In summary, we do not see any conceivable reason to split the genus *Batrachophrynus* and reject the proposal of *Lynchophrys*.

SUMMARY OF TAXONOMIC PROPOSALS

We summarized in Table VII the reassessment of the taxonomic status of central Peruvian Telmatobiinae. Three genera including seven nominal species which segregate into 15 subspecies are currently reduced to two genera *Batrachophrynus* and *Telmatobius* which include seven species without subspecific segregation.

Finally, we wish to comment on DUELLMAN's (1993) statement that the reading of *Batrachophrynus macrostomus* Peters, 1873 should be changed to *B. microstomus*. We do not agree because there is no doubt about the original naming by PETERS (1873), and in all research papers dealing with this species (AVILA RAMON, 1953; CAMARENA, 1953; DUBOIS, 1984, FJELDSA, 1983; GORHAM, 1966; LAURENT, 1983; LAVILLA, 1988a, LYNCH, 1971, 1978; MACEDO, 1950, 1960, 1976, MORALES, 1988; SINSCH, 1986, 1990; VELLARD, 1951) the original name has been used consequently.

CONVERGENT MORPHOLOGICAL TRAITS

Stream habitats require frogs to evolve morphological adaptations which enable them to move within the permanent current of water Therefore, it is not surprising that the riparian *B. brachydactylus* shares two diagnostic features with the riparian *Telmatobius*: slim head and large eye diameter. Moreover, adults of all riparian species are smaller-sized than those of the lake-inhabiting *B. macrostomus* and *T. culeus*. Confusion of these convergent morphological adaptations to the same type of habitat with similar morphology due to phylogenetic relationship has led to the creation of the genus *Lynchophrys* by LAURENT (1983). In the Andean Telmatobiinae any taxonomic conclusion based on external morphology should be backed up by other kinds of characters because the rate of erroneous classification in the morphometric distinction of the genera *Batrachophrynus* and *Telmatobius* is considerably greater than that in the distinction between stream- and lake-inhabitants: 20 % versus 8 %. Thus, the effect of convergent lines of development is probably great in this group of frogs.

GEOGRAPHICAL DISTRIBUTION

The geographical range (fig. 2) of the six central Peruvian species is still relatively unknown. We know little about the northern extension of the ranges of *T. brevirostris*, *T. carrillae* and *T. rimac*, and about the southern range of *T. jelskii*. The northern gap between the species surveyed by WIENS (1993) and those in this study is subject to a recent study (SALAS, in prep.). Further attention should be paid to the exact limits of distribution of the riparian *B. brachydactylus* in relation to those of the neighbouring *Telmatobius* species. We do not even know if *B. brachydactylus* and *T. jelskii*, both present in the hydrographic system of the Mantaro river, can coexist at the same locality.

Table VII. - Alphabetical synonymy of the telmatobiine species revised in this study.

Names in use		This study
Lynchophrys brachydactyla (Peters, 1873)		*Batrachophrynus brachydactylus* Peters, 1873
Batrachophrynus macrostomus Peters, 1873		*Batrachophrynus macrostomus* Peters, 1873
Telmatobius brevirostris Vellard, 1955		
	T. b. brevirostris Vellard, 1955	*Telmatobius brevirostris* Vellard, 1955
	T. b. parvulus Vellard, 1955	*Telmatobius brevirostris* Vellard, 1955
	T. b. punctatus Vellard, 1955	*Telmatobius brevirostris* Vellard, 1955
Telmatobius carrillae Morales, 1988		*Telmatobius carrillae* Morales, 1988
Telmatobius culeus (Garman, 1875)		
	T. culeus culeus (Garman, 1875)	*Telmatobius culeus* (Garman, 1875)
	T. culeus dispar Vellard, 1953	*Telmatobius culeus* (Garman, 1875)
	T. culeus escomeli Angel, 1923	*Telmatobius culeus* (Garman, 1875)
	T. culeus exsul Vellard, 1951	*Telmatobius culeus* (Garman, 1875)
	T. culeus fluviatilis Vellard, 1953	*Telmatobius culeus* (Garman, 1875)
	T. culeus lacustris Vellard, 1953	*Telmatobius culeus* (Garman, 1875)
Telmatobius jelskii (Peters, 1873)		
	T. jelskii jelskii (Peters, 1873)	*Telmatobius jelskii* (Peters, 1873)
	T. jelskii bufo Vellard, 1955	*Telmatobius jelskii* (Peters, 1873)
	T. jelskii longitarsis Vellard, 1955	*Telmatobius jelskii* (Peters, 1873)
	T. jelskii walkeri (Shreve, 1941)	*Telmatobius jelskii* (Peters, 1873)
Telmatobius rimac Schmidt, 1954		
	T. rimac rimac Schmidt, 1954	*Telmatobius rimac* Schmidt, 1954
	T. rimac meridionalis Vellard, 1955	*Telmatobius rimac* Schmidt, 1954

Nevertheless, there can be little doubt that the genus *Batrachophrynus* is endemic to central Perú, as already mentioned in the original description and later in VELLARD (1951). The comment on distribution in FROST (1985) – "Andes of southern Peru and Bolivia" – is obviously wrong, as is the citation of "*Lynchophrys brachydactyla*" occurring in the northern Andes of Bolivia (DE LA RIVA, 1990).

CONCLUSION

At this stage of morphometric analysis we refrain from phylogenetic considerations because of the convergent adaptations of the external morphology to the same type of habitat. In the next step of analysis, we use allozyme variation within and between telmatobiine species to approach the phylogenetic relationships and to compare them with phenetic relationships based on morphometry (SINSCH & JURASKE, 1995).

In conclusion, this paper provides an objective, diagnostic method to assign central Peruvian Telmatobiinae to the presently known species, based exclusively on external characters which are easy to measure. Thus, multivariate statistics, specifically canonical discriminant analysis, have proven again to be an useful tool in the classification of amphibians.

RESUMEN

Se revisa el estado taxonómico de los Telmatobiinae de la región central del Perú, en base a la variación intraespecífica de 18 parametros morfométricos que presentan las seis especies (con nueve subespecies) reconocidas actualmente, las cuales se agrupan en tres géneros (*Batrachophrynus*, *Lynchophrys* y *Telmatobius*). Aplicando los análises de componentes principales y de discriminación se reconocen dos géneros (*Batrachophrynus* y *Telmatobius*) incluyendo seis especies (*Batrachophrynus brachydactylus*, *B. macrostomus*, *Telmatobius brevirostris*, *T. carrillae*, *T. jelskii*, *T. rimac*) y ninguna subespecie. Dos caracteres diagnósticos y externos distinguen las especies de *Batrachophrynus* y de *Telmatobius*, otros dos son considerados adaptaciones convergentes que diferencian a los habitantes de arroyos de aquellos que habitan las lagunas

ACKNOWLEDGEMENTS

We are grateful to Lic. J CORDOVA, curator of the herpetological section of the MHNSM, Lima, and to Dr. M ORTIZ, Director of the Natural History Museum of the URP, Lima, for permitting us access to the Telmatobiinae of the local collections, especially to the type specimens assigned by J VELLARD and V MORALES M. ANTIGNANI, C. S. ARIAS, J. and F. TUEROS, and J. ICOCHEA helped us to collect frogs in the field Finally, the technical assistance of B NILOW is acknowledged. Two anonymous reviewers provided valuable comments on an earlier draft of this paper.

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APPENDIX I
SPECIMENS EXAMINED

Batrachophrynus brachydactylus

PERÚ: (1) Departamento Cerro de Pasco: Caza Pato, 9 males, 3 females, MHNSM 1311, 1314, 1316, 1319, 1324-1325, 1331-1336; (2) Departamento Junín: brook near Ondores: (a) first sample, 9 males, 10 females, URP 054-072; (b) second sample, 11 males, 11 females, collected by A. SALAS, March 26, 1992.

Batrachophrynus macrostomus

PERÚ: Departamento Junín: Junín Lake, Carhuamayo, 6 males, 7 females, 8 juveniles, collected by M. ANTIGNANI, February 20, 1992.

Telmatobius brevirostris

PERÚ: Departamento Huanuco: (1) Ambo, Chasqui, 1 male, 1 female, MHNSM 3736, 7676 (syntypes of *T. b. brevirostris*); (2) Ambo, Caina, 2 females, MHNSM 7666-7667 (syntypes of *T. b. parvulus*); (3) Santa Maria del Valle, 1 male, MHNSM 7681 (holotype of *T. b. punctatus*).

Telmatobius carrillae

PERÚ: Departamento Ancash: (1) Yuracyacu: (a) first sample, 4 males, 2 females, MHNSM 1528 (holotype), 1544-1545, 3932-3934 (paratypes); (b) second sample, 9 males,

12 females, URP 001-021; (2) Huikia: (a) first sample, 5 males, 1 female, MHNSM 6681-6687; (b) second sample, 6 males, 2 females, URP 022-029; (3) Huaychopampa, 8 males, 4 females, URP 030-041.

Telmatobius culeus

Bolivia: Lake Titicaca, Isla del Sol, 1 male, 1 female, MHNSM 7769-7770 (assigned to *T. c. culeus*).

Perú: (1) Departamento Arequipa: Yura, Arequipa, 1 female, MHNSM 7678 (syntype of *T. c. exsul*); (2) Departamento Puno: (a) Azangaro, Hacienda Checayani, 1 male, 1 female, MHNSM 7673-7674 (syntypes of *T. c. lacustris*); (b) Lake Lagunillas, 6 males, 4 females, MHNSM 7768, 7776-7777, 7785-7786, 7806-7807, 7823-7825 (assigned to *T. c. escomeli*); (c) Lake Titicaca, Ocama, 3 males, 3 females, MHNSM 7779-7784 (assigned to *T. c. culeus*); (d) Rio Coata, Juliaca, 2 males, MHNSM 7771-7772 (syntypes of *T. c. dispar*); (e) Rio Ilave, Chucuito, 1 male, 1 female, MHNSM 7754-7755 (syntypes of *T. c. fluviatilis*); (f) Rio Ilave, Huayllata, 1 male, 2 females, MHNSM 7812-7814; (g) mouth of Rio Ilave, 2 females, MHNSM 7773-7774 (assigned to *T. c. culeus*), and 3 females, MHNSM 7812-7814 (assigned to *T. c. fluviatilis*); (h) Rio Juliaca, Puno, 4 males, 4 females, MHNSM 7766-7767, 7787-7789, 7793-7794 (assigned to *T. c. dispar*); (i) Umayo, 34 km NO of Puno, 1 female, MHNSM 7811 (assigned to *T. c. lacustris*).

Telmatobius jelskii

Perú: (1) Departamento Ayacucho: (a) Ayacucho, 4 males, 6 females, MHNSM 12202, 12206, 12213-12214, 12217, 12219-12220, 12222, 12225, 12899 (assigned to *T. j. walkeri*); (b) Parinacochas, 6 males, 6 females, MHNSM 12838, 12841, 12883, 12901, 12904-12910; (c) Puquio, 2 males, 1 female, MHNSM 7642-7643, 7645 (syntypes of *T. j. longitarsis*); (d) Tambo, 2 males, 4 females, MHNSM 7646-7651 (syntypes of *T. jelskii bufo*); (2) Departamento Huancavelica: Huancavelica, 4 males, 1 female, 2 juveniles, MHNSM 7639-7641, 7660-7661, 7663-7664; (syntypes of *T. j. longitarsis*); (3) Departamento Junín: (a) Huancayo, Acolla, 3 males, 7 females, MHNSM 6903-6906, 6909-6914 (assigned to *T. j. jelskii*); (b) Huancayo, Palian, Rio Shullcas, 5 males, 2 females, 14 juveniles, collected by U. Sinsch & V. Canales, February 19-25, 1992; (c) Tarma, Cuyrohuasi: (i) first sample, 5 males, 5 females, URP 90066-90075; (ii) second sample, 6 males, 3 females, collected by A. Salas, March 24, 1992.

Telmatobius rimac

Perú: (1) Departamento Ancash: Ocros, 7 males, 3 females, MHNSM 6935-6936, 6941-6942, 6944-6945, 6950-6951, 6953-6954 (assigned to *T. r. rimac*); (2) Departamento Lima: (a) Canta, Obrojillo, Rio Chillon, 8 males, 7 females, 7 juveniles, collected by J. Icochea, March 8-9, 1992; (b) Canta, Quebrada Huaytara, 9 males, 4 females, 2 juveniles, collected by J. Icochea, March 8-9, 1992; (c) Tupe, 2 males, 2 females, MHNSM 7656-7659 (syntypes of *T. r. meridionalis*).

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International Journal of Batrachology

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GRAF, J.-D. & POLLS PELAZ, M., 1989. - Evolutionary genetics of the *Rana esculenta* complex. *In*: R. M. DAWLEY & J. P. BOGART (eds.), *Evolution and ecology of unisexual vertebrates*, Albany, The New York State Museum: 289-302.

INGER, R. F., VORIS, H. K. & VORIS, H. H., 1974. - Genetic variation and population ecology of some Southeast Asian frogs of the genera *Bufo* and *Rana*. *Biochem. Genet.*, **12**: 121-145.

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Published with the support of AALRAM
(Association des Amis du Laboratoire des Reptiles et Amphibiens
du Muséum National d'Histoire Naturelle, Paris, France).

Directeur de la Publication: Alain DUBOIS.

Numéro de Commission Paritaire: 64851.

Alytes, 1995, **13** (1): 1-44.

Contents

Alytes is printed on acid-free paper.

Alytes is indexed in *Biosis, Cambridge Scientific Abstracts, Current Awareness in Biological Sciences, Pascal, Referativny Zhurnal* and *The Zoological Record.*

Imprimerie F. Paillart, Abbeville, France.
Dépôt légal: 1er trimestre 1995.